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2 A neural pattern generator that tunes into the physical dynamics of limb system

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A Neural Pattern Generator that Exhibits Frequency-Dependent In-Phase and Anti-Phase Oscillations

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Abstract

This article describes a neural pattern generator based on a cooperative-competitive feedback neural network. The two-channel version of the generator supports both in-phase and anti-phase oscillations. A scalar arousal level controls both the oscillation phase and frequency. As arousal increases, oscillation frequency increases and bifurcations from in-phase to anti-phase, or anti-phase to in-phase oscillations can occur. Coupled versions of the model exhibit oscillatory patterns which correspond to the gaits used in locomotion and other oscillatory movements by various animals.

1 Introduction

Grillner and Zangger [3] reported that spinal cats exhibit gaits with different hind-limb phase relationships depending upon the level of electrical stimulation to the spinal cord. Tuller and Kelso [8] showed that humans cannot maintain anti-phase oscillations in a bilateral finger movement task as the required oscillation frequency is increased, but switch to in-phase oscillations at high frequencies. In various quadruped gaits, different pairs of limbs exhibit transitions from pair-wise anti-phase motion to pair-wise in-phase motion and vice-versa [6].

These and related facts about oscillatory biological movements motivate the search for an oscillator, such as the one described herein, with the following characteristics. It exhibits both 1:1 in-phase oscillations and 1:1 anti-phase oscillations. Switching between the oscillatory regimes is controlled by a single arousal parameter, I . Oscillation frequency is

*Supported in part by the AFOSR (AFOSR 90-0128)

[†]Supported in part by the AFOSR (AFOSR 90-0175) and the NSF (NSF IRI-90-24877)

[‡]Supported in part by the ARO (ARO DAAL03-88-k-0088)

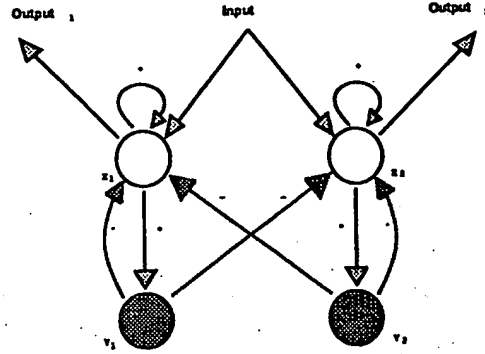


Figure 1: The two channel oscillator is capable of generating 1:1 in-phase and 1:1 anti-phase phase-locked signals for the same parameters at different arousal levels.

also controlled by this same arousal parameter. In particular, within any given oscillatory regime, faster oscillations occur for higher arousal levels. The order of oscillatory regimes can also be controlled. Parameters can be chosen such that, as I increases, either anti-phase oscillations occur before in-phase oscillations, or vice-versa.

2 The Model

The network is a version of the cooperative-competitive network introduced by Elias and Grossberg[2]. The 2-channel pattern generator, depicted in Figure 1 obeys the equations:

$$\dot{x}_1 = -Ax_1 + (B - x_1)[f(x_1) + I_1] - (C + x_1)[D_{11}g(y_1) + D_{21}g(y_2)] \quad (1)$$

$$\dot{y}_1 = E[(1 - y_1)[x_1]^+ - y_1] \quad (2)$$

$$\dot{x}_2 = -Ax_2 + (B - x_2)[f(x_2) + I_2] - (C + x_2)[D_{22}g(y_2) + D_{12}g(y_1)] \quad (3)$$

$$\dot{y}_2 = E[(1 - y_2)[x_2]^+ - y_2] \quad (4)$$

$$[\omega]^+ = \max(\omega, 0) \quad (5)$$

$$f(\omega) = F_1 \left(\frac{([\omega]^+)^2}{F_2 + ([\omega]^+)^2} \right), \quad g(\omega) = G_1 \left(\frac{([\omega]^+)^2}{G_2 + ([\omega]^+)^2} \right). \quad (6)$$

Here x_i is the activity, or potential of an excitatory neuron (population), and y_i is the activity of an inhibitory interneuron (population). The excitatory and inhibitory activities obey a shunting equation [4]. The parameters used in the simulations which produced the figures for this paper are: $A = 1.0$, $B = 1.1$, $C = 2.5$, $E = 1.0$, $F_1 = 9.0$, $G_1 = 3.9$, $F_2 = 0.5$, $G_2 = 0.5$.

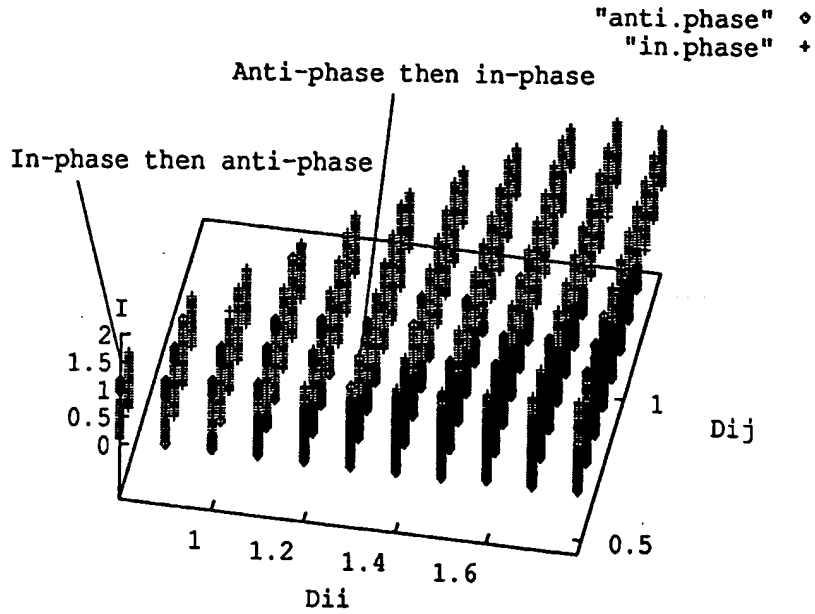


Figure 2: A plot of the oscillatory regions at different Input levels for various inhibitory coefficient levels. The relative phases were determined automatically by an algorithm which compared the relative times when the channels exceeded an output threshold, set here to 0.35. The initial conditions were *not* reset to 0 as I increased, but only at the beginning of each run, when the inhibitory coefficients were changed.

3 Heuristics for Controlling the Oscillator: Symmetry and Symmetry Breaking

Ellias and Grossberg [2] used the Hopf bifurcation theorem to study frequency dependent oscillations of (1)–(4) given a symmetric system with uniform initial data ($x_i(0) = x > 0$ and $y_i(0) = y > 0$) and uniform inputs ($I_i = I$). By symmetry, $x_1 \equiv x_2 \equiv x$ and $y_1 \equiv y_2 \equiv y$ for all time, so the system behaves like a 1-channel network. Their results proved the existence, but not the stability, of in-phase oscillations in the full 2-channel system. Conversely, if parameters are chosen such that a symmetric system approaches a stable equilibrium point, and the asymmetric 2-channel system ($n > 1$) generates stable oscillations, then these oscillations must be out-of-phase.

The above observations suggest a method for designing a neural pattern generator with both in-phase and out-of-phase oscillations. One perturbs off a 1-channel Ellias and Grossberg oscillator to create an n -channel network ($n > 1$) in a manner that reduces to the 1-channel oscillator when all initial data are symmetric. To do this, the inhibitory coeffi-

cients in (1) and (3) between the channels of the system are chosen so that $\sum D_{ji} = D$, where D is equal to the single inhibitory coefficient of the 1-channel system.

Consider an n -channel system that is stably oscillating in-phase for some value of I . Let I be changed from the value in which there are in-phase oscillations to a value in which these oscillations die out. The system is still symmetric, since $x_1 = x_2$ and $y_1 = y_2$. Thus the system reduces to the 1-channel case and converges to a stable equilibrium point. To generate out-of-phase oscillations, somehow symmetry must be broken to allow the system to move "off the diagonal." Assuming the existence of an off-diagonal orbit, how can symmetry be broken so that the system will approach that orbit and generate anti-phase oscillations?

The following methods all break symmetry: Asymmetries in the inhibitory coefficients, noise, asymmetries in the inputs, and asymmetries in any other parameters of the channels. Systems with asymmetric interaction coefficients are less flexible than symmetric systems for generating both in-phase and anti-phase oscillations. Asymmetries in the inhibitory coefficients do facilitate switching. Anti-phase oscillations may also be achieved by introducing perturbations via other asymmetries; for example, in the arousal channel. There are two ways to change the way arousal enters the system, yet still get the arousal from a single command source:

1. Make one input channel stronger than the other; e.g. let $I_1 = I$ and $I_2 = I + \delta$.
2. Make the onset of equal I_1 and I_2 inputs asynchronous. That is, $I_1 = I_2 = I$ first activate each channel at slightly different times. In our simulations, this lag was .001. This scheme produces a transient asymmetry, which is automatically scaled by the arousal level.

Mechanism (1) produces a spatial asymmetry in the oscillator. Mechanism (2) produces a temporal asymmetry in the oscillator. As shown below a small asynchrony in the arousal arrival time produces anti-phase oscillations for many values of the parameters. The only parameters that were varied in the simulations were the inhibitory coefficients, D_{ii} and D_{ij} , and the arousal level I .

4 Simulation Results

The system exhibits both 1:1 in-phase and 1:1 anti-phase oscillations. Anti-phase oscillations occur for values of I which bracket the values for which in-phase oscillations occur. The system can also be designed to always go to a stable point, for example by increasing the inhibitory averaging rate E in (2) and (4). Then (1)-(4) reduce to a Cohen-Grossberg model, which always approaches equilibrium [1].

Figure 3 shows a series of runs for two oscillators using the same values of I for both runs. In Figure 3A, the in-phase orbits precede the anti-phase orbits as oscillation frequency increases. In Figure 3B, anti-phase oscillations precede in-phase oscillations, as in the data of Tuller and Kelso [8].

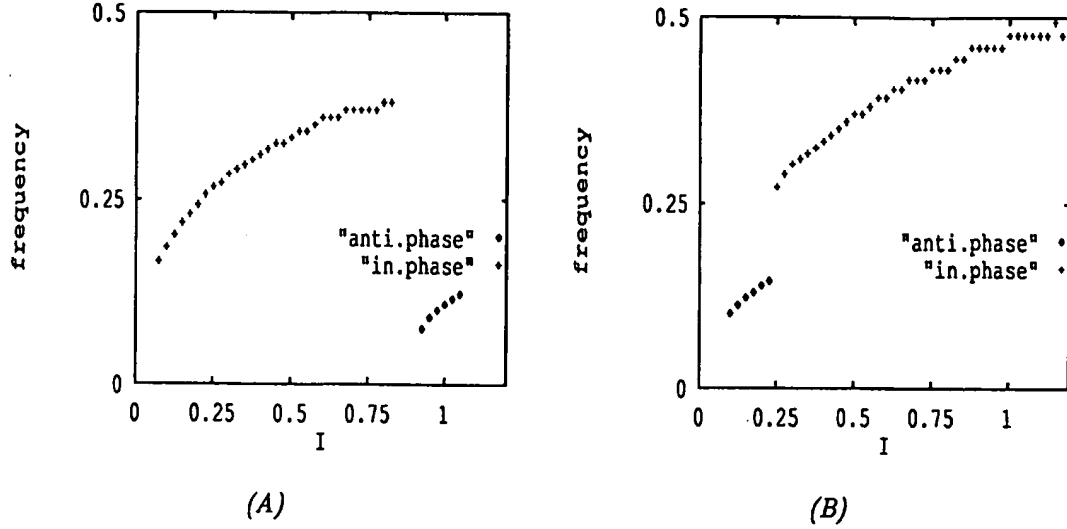


Figure 3: Frequency plots for: (A) In-phase to anti-phase: $D_{ii} = 0.8$, $D_{ij} = 0.45$, Anti-phase to in-phase: (B) $D_{ii} = 1.3$, $D_{ij} = 0.55$. The initial conditions were reset at each I increment.

Figure 4 illustrates waveforms of the oscillations summarized in Figure 3. Note the sharp peaks in the anti-phase waveform in Figure 4B. Compare these with the broad plateau waveforms of the anti-phase waveform of Figure 4A. In our simulations, these waveforms are fairly consistent; that is, anti-phase orbits which precede in-phase orbits tend to have sharp peaks and those which occur after in-phase orbits tend to be plateau-like. This is a useful property, because it yields a third degree of freedom in addition to phase and frequency, namely waveform shape. This property may be used, for example, in controlling transitions between walking and running in bipeds. These two gaits have the same relative phase, but different qualitative behavior.

The sigmoid activation function in (6) can generate both in-phase and anti-phase oscillations with the same parameters for different arousal levels. If, on the other hand, $f(\omega)$ and $g(\omega)$ are chosen faster-than-linear, say, $f(\omega) = F([\omega]^+)^2$ and $g(\omega) = G([\omega]^+)^2$, then only in-phase oscillations were found in many parameter ranges. Anti-phase oscillations may exist, but for a much narrower range of parameter selections. The LSODA numerical integration package [7] provided accurate numerical integration.

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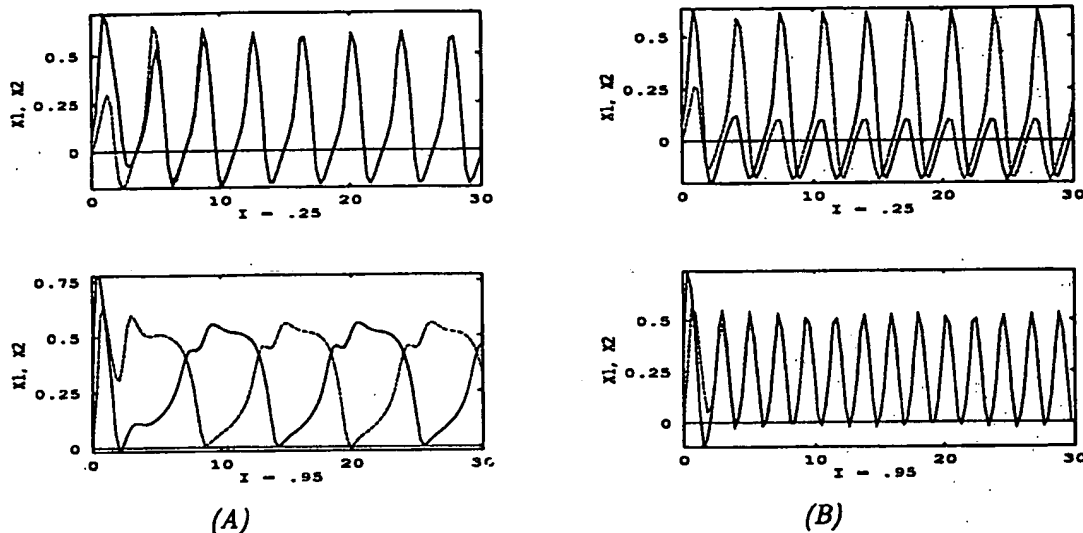


Figure 4: (A) shows plots from a sequence of I 's for: $D_{ii} = 0.8$, $D_{ij} = 0.45$. The in-phase oscillations occur for lower values of I than do the anti-phase oscillations. (B) shows plots from a sequence of I 's for: $D_{ii} = 1.3$, $D_{ij} = 0.55$. The anti-phase oscillations occur for lower values of I than do the in-phase oscillations. Observe the shapes of the anti-phase waveforms in both (A) and (B). The initial conditions were reset in all plots.

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